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A CLASSIFICATION AND PHYLOGENY OF THE ELASMOBRANCH FISHES

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The classification presented here is the result of extended research covering several years. The work was originally undertaken at the suggestion of Dr. W. K. Gregory, Curator of Ichthyology at The American Museum of Natural History in New York City, and the museum collections have been at my disposal at all times.

While engaged in this work it became apparent to me that the Order Galea was in need of complete reorganization, and in order to supplement the material available, I took an extended trip during a year's sabbatical leave to study the sharks of the Pacific and Indian Oceans. In 1930, I spent several months in Japan, where the collections of the Imperial University at Tokyo were placed at my disposal. Fresh sharks were also obtained from the markets, and some weeks were spent at the Marine Biological Laboratory at Misaki where very large specimens were obtained directly from the fishermen. In 1931 I spent several months in Java where the large wholesale markets made available sharks from a wide area. Here, also, I was able to examine an extensive collection at the laboratory maintained by the Dutch Government at Batavia. As the time at my disposal was limited it was not possible to include the Australian or Mediterranean types, but through the courtesy of Dr. T. Marini of Buenos Aires, who visited the Museum in New York in 1932, I was able to examine his collection of South American elasmobranchs, and to make the necessary dissections upon them.

A large number of specimens have been examined, therefore, both internally and externally, with many interesting results. The present publication is a mere prodromus of the complete report which is now ready for publication with illustrations, tables, and explanatory material. Full definitions and bibliography have therefore been omitted from this report.

I wish to express my appreciation at this time to Dr. W. K. Gregory and his associates of the Department of Ichthyology of The American Museum of Natural History in New York City for their cordial coöperation with this work at all times, and for the research facilities provided

at the Museum, and the contacts establishing during the years spent abroad.

To Dr. Naohide Yatsu, Dr. Negumi Eri, and Dr. Shigeho Tanaka who in 1930 made my stay in Japan a pleasant and profitable one, and especially to Dr. Tanaka for the invaluable material from his collections.

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To Dr. T. Marini, Guggenheim Fellow from Buenos Aires, for the loan of his South American collection in 1932.

The term Superclass is used for the Pisces and Class for the Chondropterygia. The class is defined as follows: exoskeleton of dermal denticles structurally identical with the teeth; spines primitively present; ceratotrichia present, lepidotrichia absent; endoskeleton cartilaginous, often calcified; membrane bone absent; elements of skull not separated by sutures; primary lower jaw (Meckel's cartilage) principal element; spines of pectoral arch absent, no bone cells in the arch; ribs typically of dorsal type; notochord more or less persistent; vertebral column with neural and haemal arches only; branchial arches 5–7; branchial openings separate, without opercula (except Chismopnea); paired nasal organs, each with one external opening; no air bladder or lungs; modern forms with internal fertilization and myxopterygia in the male.

Endings of parallel groups have been made uniform according to the following series; for Class "ia," for Subclass "i," Superorder "eae," Order "ea," Suborder "ida," Superfamily "oidea," Family "idae."

The basis of division between groups is determined by groups of characters. It is my belief that the deep-seated internal structures have a greater significance phylogenetically than the external characters which have fluctuated with changing environments. The latter have been used, therefore, for the most part to distinguish between genera and species, and the former between the larger groups.

KEY TO THE ORDER GALEA

I.—Nictitating membrane absent; vertebral centra with four main uncalcified areas without calcified rods; radiating calcifications in the calcified areas, frequently branching, or rarely, with concentric laminae.....SUBORDER ISURIDA.

A.—First dorsal posterior to the pelvics; rostral cartilages short,

not united; pectoral fins with radials on the mesopterygium and metapterygium about equal.

AA.—Caudal axis low; expanded propterygium and mesopterygium.....SUPERFAMILY ORECTOLOBOIDEA.

B.—First dorsal anterior to the pelvics; rostral cartilages three united; pectoral fins with radials mostly on the metapterygium. SUPERFAMILY ODONTASPOIDEA.

BB.—Caudal axis low; small propterygium and mesopterygium.....SUPERFAMILY ISUROIDEA.

II.—Nictitating membrane present or rudimentary; vertebral centra with calcified rays extending into each of the four main uncalcified areas; secondary calcifications in the form of a maltese cross; or vertebral centra showing all stages of development of type; rostral cartilages three, united; pectoral fin with well-developed propterygium and mesopterygium; caudal axis low.

SUBORDER CARCHARINIDA.

A.—Nictitating membrane rudimentary; vertebral centra showing all stages of development of type; oviparous.

SUPERFAMILY CATULOIDEA.

B.—Nictitating membrane more or less perfectly developed; vertebral centra of complete maltese cross type; ovoviviparous.

SUPERFAMILY CARCHARINOIDEA.

CLASSIFICATION

Superclass Agnatha
Superclass Pisces
  Class Chondropterygia (elasmobranch fishes)
    Subclass Stegoselachi (armored sharks)
      Superorder Stegoselacheae
        Order Stegoselachea
          Family Macropetalichthyidae (Devonian)
          Family Cratoselachidae (Carboniferous)
    Subclass Rhenandini
      Superorder Rhenandineae
        Order Rhenandinea
          Family Gemündinidae (Devonian)
    Subclass Pleuropterygii
      Superorder Pleuropterygeae
        Order Cladodea
          Family Cladoselachidae (Devonian, Carboniferous)

Family Symmoriidae (Devonian, Carboniferous)
Family Ctenacanthidae (Devonian-Permian)
Subclass Ichthyotomi
Superorder Pleuracantheae
Order Pleuracanthea
Family Pleuracanthidae (Permian)
Subclass Plagiostomi (sharks and rays)
Superorder Antaceae (sharks)
Order Hexanchea
Suborder Hexanchida
Superfamily Hexanchoidea
Family Chlamydoselachidae
Family Hexeptranchidae
Order Galea
Suborder Isurida
Superfamily Orectoloboidea
Family Orectolobidae
Family Rhineodontidae
Superfamily Odontaspoidea
Family Carchariidae
Family Scapanorhynchidae
Superfamily Isuroidea
Family Vulpeculidae
Family Isuridae
Family Cetorhinidae
Suborder Carcharinida
Superfamily Catuloidea
Family Catulidae
Family Halaeluridae
Family Atelomycteridae
Superfamily Carcharinoidea
Family Triakidae
Family Galeorhinidae
Family Carcharinidae
Family Sphyrnidae
Order Heterodontea
Suborder Heterodontida
Superfamily Heterodontoidea
Family Heterodontidae

- Suborder Hybodontida
  - Superfamily Hybodontoidea
    - Family Hybodontidae (Triassic, Jurassic)
- Suborder Edestida
  - Superfamily Edestoidea
    - Family Edestidae (Carboniferous, Permian)
- Order Squalea
  - Suborder Squalida
    - Superfamily Squaloidea
      - Family Squalidae
      - Family Echinorhinidae
      - Family Scymnorhinidae
    - Superfamily Pristiophoroidea
      - Family Pristiophoridae
  - Suborder Rhinida
    - Superfamily Rhinoidea
      - Family Rhinidae
- Superorder Platosomeae (rays)
- Order Narcobatea
  - Suborder Narcobatida
    - Superfamily Narcobatoidea
      - Family Narcaciontidae
- Order Batea
  - Suborder Batida
    - Superfamily Rhinobatoidea
      - Family Rhinobatidae
      - Family Pristidae
      - Family Discobatidae
    - Superfamily Rajoidea
      - Family Rajidae
    - Superfamily Dasybatoidea
      - Family Dasybatidae
      - Family Potomotrygonidae
      - Family Myliobatidae
      - Family Rhinopteridae
      - Family Mobulidae

Subclass Bradyodonti

- Superorder Bradyodonteae
  - Order Bradyodontea
    - Suborder Bradyodontida

Family Petalodontidae (Devonian, Carboniferous, Permian)
Family Cochliodontidae (Devonian, Carboniferous, Permian)
Family Psammodontidae (Carboniferous)
Family Copodontidae (Carboniferous)
Subclass Ptyctodonti
Superorder Ptyctodonteae
Order Ptyctodontea
Suborder Ptyctodontida
Family Ptyctodontidae (Devonian, Mississippian)
Subclass Holocephali
Superorder Chismopneae
Order Chimaerea
Suborder Chimaerida
Superfamily Callorhynchoidea
Family Callorhynchidae
Superfamily Chimaeroidea
Family Chimaeridae
Family Rhinochimaeridae
Order Squalorajea
Suborder Squalorajdia
Superfamily Squalorajoidea
Family Squalorajidae (Jurassic)
Family Myriacanthidae (Jurassic, Cretaceous)
Class Acanthodia
Class Osteopterygia

ORDERS OF THE ANTACEA

	HEXANCHEA	HETERODONTEA	SQUALEA	GALEA
Dorsal fins	1	2	2	2
Dorsal fin spines	absent	present	present	absent
Anal fin	present	present	absent	present
Gill openings	5–7	5	5–6	5
Sixth gill arch	complete	absent	absent or complete	rudimentary
Jaw suspension	amphihyostylic	amphihyostylic to hyostylic	hyostylic	hyostylic
Pterygoquadrate articulation	loose	extensive	absent	loose or absent
Palatobasal process	present	present	absent	reduced
Rostral cartilages	single	absent	single	triradiate
Pectoral fin				
Mesopterygium	on margin of fin	not on margin	not on margin	not on margin
Radials on propterygium	none	1	1–several	1–several
Radials on mesopterygium and metapterygium	equal	about equal	about equal	unequal
Notochord	unconstricted anteriorly	constricted	constricted	constricted
Vertebrae	diplospondylic	monospondylic	monospondylic	monospondylic
Vertebral centra	undifferentiated anteriorly, asterospondylic posteriorly	modified tectospondylic	cyclo- or tectospondylic	asterospondylic
Myxopterygia				
Elements of stem	2	2	1–2	1
Axial cartilage	cylindrical and pointed	cylindrical and pointed	cylindrical and pointed	dorso-ventrally flattened
Ventral marginal	short and distal	short and distal	short and distal	elongate

THE PHYLOGENY OF THE ELASMOBRANCHS

Modern elasmobranchs are a survival of a Paleozoic race, relatively unsuccessful as fishes, but of interest because they link the jawed vertebrates with the earliest known Agnatha. These were an armored race of jawless vertebrates appearing sporadically in the early Silurian for-

mations, becoming abundant in the late Silurian and Devonian, and becoming extinct at the close of the Devonian. Great progress has been made in the last decade or so due to the discoveries of Danish, Norwegian, and Swedish expeditions to Spitzbergen, East Greenland, and adjacent regions. The superb material thus revealed has enabled Stensiö to give accurate descriptions of the chambers containing the central nervous system and of the tubes transmitting the nerves and blood vessels of the head. The labors of Stensiö and Kiaer have resulted in many far-reaching conclusions concerning the relationships of these early forms.

Two groups are important phylogenetically: the Osteostraci which lead to the modern cyclostomes, and the Heterostraci which may lead to the elasmobranchs. The head and thorax are characteristically encased in an armor composed of a dorsal shield and a ventral shield, and sometimes two lateral shields. The abdominal region is covered with separate overlapping plates or with minute denticles. The axis of the tail is typically hypocercal, the axis of the body turning down.

The material of the shields on microscopic examination shows four layers of tissue: a basal layer which in the Osteostraci contains true bone cells, a cancellated layer, a reticular layer, and an external layer of dentine. The canals of the lateral line system pass through the reticulated layer and open by pores on the outside. On the ventral surface of the dorsal shield impressions of the internal structure are often found, showing the course of the lateral line system, the nasal openings, and the gill pouches. Some endoskeletal elements are found, and the brain case and nerves have been traced out.

In the Osteostraci there are numerous gills, from nine to fifteen, several of which lie anterior to the region of the spiracle in fishes. Each has a separate opening on the ventral surface. There is a single median nasal opening on the dorsal surface just back of the pineal impression, and the two very small orbits lie close together behind it. Stensiö has worked out the anatomy of cephalaspids in detail and finds that all the cavities and canals are lined with bone cells. The brain case, head shield, and gill cavities, all suggest the modern *Petromyzon*, as do also the single dorsal nasal opening and the two semicircular canals in the ear. Thus the cyclostomes today are a degenerate race, but are no doubt a survival of this ancient group.

The Heterostraci are less specialized and more primitive. They are very small, depressed grovellers, without appendages. The gills are only six or seven in number, and there is a single opening for them on

each side. The mouth is a slit on the ventral surface and the nasal opening seems to be within the slit. In rare cases two nasal sacs are reported. The armor has no bone cells and the dorsal shield varies from a single piece in *Poraspis* to minute denticles in *Thelodus*. Kiaer suggests that the single piece as found in *Poraspis* is primitive, and that the separate plates are due to the breaking up of the shield. Smith Woodward suggests that the shape of the plates is directly due to the arrangement of the soft parts underneath, but he believed (1915) that the plates are due to the fusion of the small denticles. If Kiaer is correct, the movements would serve to break up the plates, and the following series can be pictured.

Anglaspis has a dorsal shield with raised ridges of dentine forming a pattern. In *Cyathaspis* the shield is divided into four regions by distinct limits in the dentine layer. In *Pteraspis* the plates are separate and symmetrically arranged with fine concentric ridges, and in *Tolypaspis* the shield is broken into numerous small discs, each with a stellate ornamental peak, possibly representing the origin of the denticle. In *Thelodus* and *Lanarkia* the plates are all small, separate tubercles resembling the shagreen of the elasmobranchs. They are too specialized to represent a stage in the succession for they are extremely depressed at the anterior end, but they are found very late in the Silurian and so may well be derived forms.

Two groups of jawed vertebrates appeared in the late Silurian, both probably derivatives of the Heterostraci. The arthrodires were a grovelling group and the whole body was encased in a bony armor; the acanthodians were fusiform, fishlike forms in which the armor was composed of small quadrangular plates, larger on the head, and covered with a substance like ganoine, suggestive of the higher fishes. Fishlike paired and unpaired fins were present, all spiny, and in some forms accessory paired fins appeared. The spines have a remnant of the tubercular armor on their front margins, and each of the five pairs of gills has a separate opercular covering. These have sometimes been classed as sharks but the differences are too great. There is very little axial endoskeleton, and no endoskeletal support for the fins.

The elasmobranchs first appear in the lower Devonian. Probably the most primitive known is the small marine *Macropetalichthys prümiensis* (E. Kayser). This was an armored shark retaining a dorsal shield composed of several bony plates but having an endoskeleton well preserved and distinctly on the elasmobranch plan (Broili, 1933). The body is depressed anteriorly but not extremely so. It dwindles to a

point at the tail with no unpaired fins, but the paired fins are large and have complete endoskeletal supports. That of the pectoral fins is of especial interest. There is a complete pectoral arch on which the three basals articulate. The metapterygium was not wholly preserved in the fossil but the shape of the piece found indicates that it was expanded like the mesopterygium and propterygium. All three were about the same size. Three unsegmented radials were preserved from the size of which it would seem that there were radials attached to all three basals and about as many on the mesopterygium as on the metapterygium. This is characteristic of the more primitive of the existing forms today, except that in all the modern sharks the radials are segmented into two or more pieces.

Such a fin appearing at this early period suggests the possibility that the paired fins of fishes had their origin from the Agnatha where the lateral appendages, when present, are outgrowths of the carapace. A primitive suggestion of such an outgrowth is found in *Anglaspis*, the heterostracian. The finely ridged dorsal shield is undivided but slight, blunt projections extend out from either side at about the position of the pectoral fins of fishes. Among the Osteostraci more definite appendages are found. In *Cephalaspis* the carapace curves in at this same region to form what is called the pectoral sinus, and from this point on each side a fleshy flap protrudes. If these represent primitive paired appendages, then the endoskeleton was a later development, probably due to the movements of the underlying muscles, and the three basal cartilages had a simultaneous origin. This is contrary to Balfour's theory of fin development in which the metapterygium is supposed to be older than the other two basals.

Smith Woodward (1915) considers the fusiform shape with the anterior dorsal fin as primitive, and believes that pelagic life preceded the grovelling life in any group. In the modern sharks, however, the slightly depressed groups retain more archaic characters than the fusiform, and, looking back through the geological record we can see that the grovellers must always have preceded the swimmers if only from the abundance of food on the bottom. Whether in fresh water or salt, invertebrates were the only source of food, and the first experiments toward vertebrate structure must have occurred where invertebrates were plentiful. This was not out in the open waters, and any attempts to venture into deeper waters must have been preceded by successful life near shore. It was only a few grovelling types which survived the close of the Devonian and, again, at the close of the Permian, when the

seas became practically devoid of animal life, it was the occasional grovelling elasmobranch which carried the race over the famine period to the more abundant Jurassic.

Therefore, the small grovelling forms may be looked upon as ancestral to any other type of vertebrate life, whether tending toward deep-sea types or more extreme bottom-living types. Romer has suggested that the heavy armor of the early forms may have been necessitated by the activities of the large voracious eurypterids, for these scorpion-like invertebrates were abundant during the same periods, and some were larger in size than many of the Agnatha. The Silurian vertebrates have left no clear record of chronology, but such specimens as have been found in the scattered remains of the earlier formations have been grovelling types such as *Cephalaspis*. No fusiform-shaped forms, either of the agnathan Anaspida, or of the acanthodians, appeared until the late Silurian formations when all of the known types are found in formations of about the same geological age.

Therefore, the facts do not preclude the grovelling type as primitive, and *Macropetalichthys* answers all requirements as a plausible ancestral type of the elasmobranchs. The earlier history must have been passed in the upper Silurian, parallel with the acanthodian development, but no record has been yet discovered. The armored elasmobranchs, or Stegoselachians, were not a large group, but they occur sporadically as late as the Carboniferous, when *Cratoselache* with its greatly reduced dorsal shield became extinct. *Gemündina*, a curiously specialized type with flattened and expanded pectorals very similar to the modern monkfish, occurred at a period slightly earlier than *Macropetalichthys* and shows that the tendency for reduction of the armor had begun at an earlier date. *Gemündina* has a large terminal mouth. The dorsal head shield has lost the central plates and the lateral head plates are fenestrated. The endoskeleton is quite plainly elasmobranchian.

In the late Devonian are found the first true elasmobranchs in which all that remains of the armor is the covering of dermal denticles and the dorsal fin spines. The spines are often greatly ornamented with dentine ridges and rows of tubercles. Tooth development determined the success of the group. In *Cladodus*, which is recognized as the central type, the teeth have a very broad base which is deeply embedded in the tissue of the jaw. There is a strong upright central cusp and numerous smaller upright lateral denticles. The teeth of *Macropetalichthys* were flat, round discs folded over the edge of the flat mandible. These may represent the base of the elasmobranch teeth, the cusps arising as ridges

of dentine arose on the carapace of the Agnatha. All of the Paleozoic elasmobranch teeth retained the broad base, only the Cretaceous sharks acquiring the two-rooted base which is less securely fixed to the jaw.

Cladoselache was a somewhat elongate deep-sea representative of the cladodonts. It was highly specialized and became extinct at the close of the Devonian. By some it has been looked upon as the primitive elasmobranch, but if the fin of *Macropetalichthys* is primitive, then the wide-based fins of *Cladoselache* are a specialization.

The tooth structure of *Cladodus* was successful if the fusiform shape was not, for all other known types of elasmobranch teeth can be traced back to this broad-based multicusped type. During the Carboniferous age tooth structure underwent specializations toward all types of environment. The only fusiform type was the very elongate *Pleuracanthus* which survived for a short time in the Permian and became extinct at the close of that period. The other types were all grovellers and the teeth were variously modified for grinding hard objects such as mollusc shells.

The Bradyodonti are a group apart but, according to A. S. Woodward, they probably lead to the modern chimaeras. Their broad-based teeth had slightly rounded crowns. These were crowded close together to form flat crushing pavements which were most effective in attacking mollusc shells. The teeth were largely composed of tubular dentine, a structure quite different from that of the ordinary elasmobranch teeth but found in the tritors of the modern *Chimaera*. The group includes *Petalodus*, *Cochliodus*, and *Psammodus*. None survived the Permian and no Triassic link has been found, but *Ganodus* and *Squaloraja* which appeared in the Jurassic lead direct to the chimaeras and must represent the survival of some such group in the Permian.

As the bases of the teeth were firmly embedded in the jaw it was not as easy for the series of teeth moving up to the margin to drop off as do the teeth of modern sharks, and this may account for the tendency toward fusion of the series. This reached its extreme in the symphyseal teeth of the edestids which protruded from the mouth in long spirals of fused teeth. *Edestus* and *Helicoprion* are extreme examples.

The teeth of *Notidanus* which appeared first in the Jurassic must have had their origin in the Carboniferous teeth. Here there is a differentiation between the teeth of the upper and lower jaws; those of the lower jaw having cusps in a receding series on an elongate base instead of a central cusp. This is not difficult to derive from the cladodont type, and their origin must have been from the stem forms in the Carboniferous before the hybodont teeth became established.

Orodus had obtuse elongate teeth with the dental crown raised in the middle. The surface was marked with more or less prominent wrinkles of dentine which rose from each long margin or from a median longitudinal crest. It was a crushing type but not fused into pavements. Toward the center the teeth retained a more cuspidate structure. It was this heterodont dentition which enabled the hybodonts to survive the extinction which closed the Paleozoic, when the dearth of food caused by the extinction of the invertebrates made life impossible for the vertebrates also.

There was little life in the early marine Mesozoic waters, but during the Triassic small bony fishes began to increase in numbers. The only elasmobranchs found are the hybodonts of which *Hybodus* is the Triassic type. The body is depressed and enlarged forward not unlike the modern Port Jacksons. In the Carboniferous types the dorsal fin spines were ornamented with ridges, but in *Hybodus* they are practically smooth and enamelled. The teeth are definitely heterodont, the central teeth being quite sharply cusped.

By the opening of the Jurassic food was again abundant and the elasmobranch fishes began once more diverging actively in all directions. This time the types were successful, for nearly all the Jurassic families are represented among the recent forms. Probably all of the fundamental skeletal changes were established during the Jurassic, and small specimens which have been found in the Lithographic stone of Bavaria have been most instructive even though lacking in many important skeletal details. The teeth are conspicuously absent from these fossils. Possibly this marks the change from the deeply embedded teeth, and if they were quite small and fragile they would have been less likely to be preserved. In the Cretaceous formations innumerable shark teeth are found often quite separate from the specimens, but these are all so like the modern forms that it is unfortunate that the linking types have not been preserved.

Some clue to their structure may be had from *Palaeospinax*, a hybodont of decidedly more modern character which appeared in the late Triassic or Liassic. It still retains the enamelled spines and the heterodont teeth, but the symphyseal teeth are very sharply cuspidate with only one pair of small lateral denticles, and the lateral teeth are low-crowned with several lateral denticles reduced to minute beads.

The vertebrae, too, diverged during this period. Knowledge of fossil vertebrae is scant and unsatisfactory and is usually from surface descriptions. Smith Woodward (1919) describes the vertebrae of

Palaeospinax as faintly asterospondylic, and Dean describes them as strongly cyclospondylic. In *Protospinax*, Smith Woodward describes concentric laminae which are characteristic of many of the squaloid sharks. It is a tectospondylic type. In *Crossorhinus jurassicus* he describes some calcification around the primitive double cone which would perhaps be a cyclospondylic type. No description is offered of the vertebrae of *Crossorhinops minus* (*Palaeoscyllium minus* Smith Woodward) or of *Palaeoscyllium formosum* Wagner (1861), but *Pristiurus* which is found in the later Jurassic had cyclospondylic vertebrae.

Among the modern groups the tectospondylic type with either concentric laminae or irregular radiations but without four main uncalcified areas is found in the Heterodontea (Port Jacksons), and in many of the Squalea and rays. The cyclospondylic type is found in the more typical of the Squalea and in the more primitive of the Catuloidea. The asterospondylic type is confined to the Galea, and two patterns have developed. In the Isurida, which includes the Orectoloboidea, the Odontaspoidea, and the Isuroidea, the calcifications are radiating, often branching, but always avoiding the four main uncalcified areas; in the Carcharinida, including the Catuloidea and the Carcharinoidea, the type has the calcifications in the form of a maltese cross with four short, stiff rods extending into the four main uncalcified areas. In the Catuloidea several stages exist between the purely cyclospondylic and the maltese cross type.

It is probable, therefore, that the type predominating in the Jurassic was cyclospondylic, and that any variation from that was toward the tectospondylic as found in the Heterodontea. As the radiations in this type resemble the asterospondylic in surface view, references to asterospondylic vertebrae in the Hybodontea may be taken to mean tectospondylic.

In deriving the modern groups from the Jurassic types only surface resemblances can be depended upon as the teeth are entirely lacking and the skeletal remains scant. *Protospinax* has the skeleton of the pectoral fin not far removed from that of *Macropetalichthys*. It is a type characteristic of the Squalea, and of the Orectoloboidea and Odontaspoidea of the galeoid sharks. These may therefore all be derived from *Protospinax* or some similar form. *Protospinax* has retained the spiny dorsal fins and the anal fin from the hybodonts. The position of the anal, and its small size, as well as the position of the dorsal fins, is paralleled in these small Jurassic forms by *Crossorhinops minus* and by *Crossorhinus jurassicus*. These two types have depressed heads, and

in *Crossorhinus* there are three pairs of dermal lappets. The general form is that of the modern *Orectolobus* which is a bottom living shark, primitive in many respects, and leading to both the Odontaspoidea and the Isuroidea. If *Protospinax* is the origin of this line, and if the concentric laminae in the vertebrae are the primitive squaloid type of vertebra, then the radiating calcifications of the Isuroidea may have risen from the tectospondylic and not directly from the cyclospondylic. This might explain the appearance of concentric laminae in the vertebrae of the two gigantic sharks, *Cetorhinus* and *Rhineodon.*

It is difficult to reconcile Smith Woodward's figure of his *Palaeoscyllium minus* with the *Palaeoscyllium formosum* of Wagner. There is so little resemblance, that I have changed the name of this type to *Crossorhinops minus* to show the much closer resemblance to the specimen of *Crossorhinus jurassicus* described by Smith Woodward. The small size and position of the anal fins is alike in both and quite different from *Palaeoscyllium formosum.* This latter type is more like the Catuloidea which group includes the *Scyllium* of Cuvier although that name has been abandoned in favor of *Catulus.*

The catuloids then show greater resemblance to *Palaeospinax* than to *Protospinax* and the Carcharinida would be less closely related to the Squalea than the Isurida, but probably derived from the same hybodont line. Since Dean describes the vertebrae of *Palaeospinax* as strongly cyclospondylic, and the vertebrae of the modern Catulidae are of that type, this origin is quite probable.

Except that they have lost the anal fin, the Squalea are very similar to *Protospinax.* The divergence to the Rhinidae was, also, started in the Jurassic with *Squatina,* and from these all of the modern rays may have been derived. All of these groups retained the larger spiracle which was an adaptation to shallow water breathing.

The Cretaceous saw the establishment of the more highly specialized families: *Odontaspis* founded the Carchariidae, *Oxyrhina* and *Lamna* the Isuridae, *Corax* the Cetorhinidae; thus, the Isurida, which was started by the Orectolobidae in the Jurassic, were all well on their way. Among the Carcharinida, which were begun by the Catulidae in the Jurassic, *Catulus* (*Scyllium*) represented the Catulidae and *Galeorhinus* (*Mustelus*) established the Galeorhinidae, but the large group of voracious sharks were not established until the Eocene when *Galeocerdo* and *Carcharinus* appeared. The Sphyrnidae are reported in the Eocene but were not well established until the Miocene.

Thus the more highly specialized the group of sharks, the later has

been their appearance geologically, and the entire group of modern sharks can be traced back, even over the break that closed the Paleozoic to the Devonian, and through the Devonian elasmobranchs to the Silurian Agnatha. While not the most successful group of fishes, therefore, they have had a longer history of survival than any of the bony fishes.